THE NUMBER OF PRE-ADULT INSTARS, GROWTH, RELATIVE GROWTH, AND VARIATION IN DAPHNIA MAGNA

BERTIL GOTTFRID ANDERSON [1]

Biological Laboratory, Western Reserve University

Until recently growth and variation in Crustacea have been studied by means of preserved materials. These materials may consist of a single collection taken in a certain locality at a specific time or several collections made in different localities at different times. Often conclusions are drawn from an isolated collection. Such studies necessarily neglect the past history of the individual. Any conclusions reached by such methods regarding growth and variation can only be regarded as tentative and subject to verification by experiments with individually reared animals.

As a result of such studies on *Coronis*, Brooks (1886) was led to the statement: " . . . the length of the larva increases uniformly at each moult by one fourth of its length before the moult." Later Fowler (1909) designated this numerical relation " Brooks' Law." He also called the fixed fractional increase the " growth factor."

That " Brooks' Law " does not hold for Cladocera has been shown by Rammner (1930) after a series of studies on individually reared animals from several genera. Gurney (1929) doubts that the above relations exist for copepods. Other arthropods as well do not follow " Brooks' Law." Calvert (1929) found that larval Odonata grow quite irregularly.

Such studies with Cladocera have perhaps led to the conclusion that individuals of a species pass through a definite number of pre-adult instars. When a graph of a population is made wherein the number of individuals of a size class is plotted against size, *i.e.*, total length, a series of size modes is secured (Fig. 1). These size modes are taken as representative of the growth stages of the organism. Usually females of a given species which are of a specific size or larger bear eggs in their brood chambers. The number of size modes between the embryonic stages and the mode of the smallest egg-bearing females is taken as the number of pre-adult instars for the species.

[1] A part of the experimental work related in this paper was done at the Zoölogical Laboratory of the State University of Iowa.

Inspection of graphs of size distributions such as in Fig. 1 shows that the size groups represented by the modes are not entirely distinct. The size groups in the lower size ranges are usually quite distinct but not decidedly disjoined from each other. Those in the higher size ranges

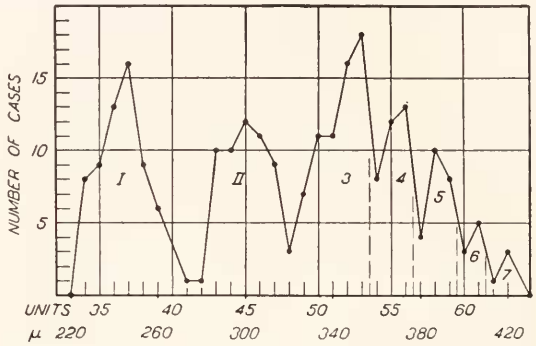

FIG. 1. Distribution of a population of *Chydorus sphæricus* according to length (after Werner).

tend to run together and are not so easily identified. Since the size groups are not entirely distinct over the pre-adult range and the past history of each individual is not known, the conclusion that all indi-

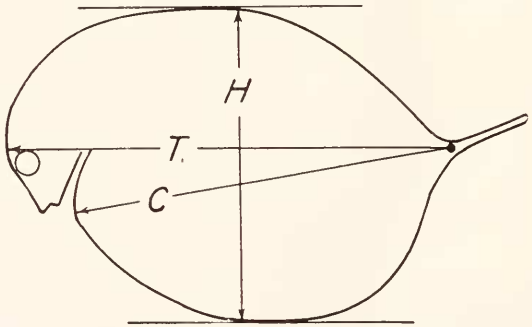

FIG. 2. Diagram showing methods of making measurements. *T*—total length, longest dimension of animal exclusive of spine. *C*—carapace length, longest dimension of carapace exclusive of spine. *H*—height, the shortest distance between two lines tangent to the carapace, as illustrated, and parallel to the line of *T*. This measure of height is affected but little by the number of young in the brood chamber.

viduals of a species have a definite number of pre-adult instars is not necessarily valid.

The writer finds that the number of pre-adult instars for *Daphnia magna* is rather variable. Calvert (1929) reported that the number of larval instars for certain species of Odonata is not constant. Dover (1931) reported that the number of moults in *Orgyia turbata* decreases

when fed on *Crotolaria*. Singh-Pruthi (1925, etc.) found that the number of moults for mealworms can be varied. Schubert (1929) examined *Ceriodaphnia reticulata* from two ponds. The material from the one pond was collected early in July, 1926. He believed that all *C. reticulata* in this collection were primiparous in the fourth instar. The material from the second pond was taken in mid-September of the same year. His findings regarding the latter were that 60 per cent of the individuals were primiparous in the third instar and that 16 per cent were still immature in the fourth. He concluded that at least two varieties of *C. reticulata* exist in these ponds. Apparently the number of pre-adult instars is variable in this species. Agar (1930) reports that *Simocephalus gibbosus* and *Daphnia carinata* have three and four pre-adult instars respectively but adds that a small percentage of the individuals become mature in one less than the average.

The aim of this paper is to present data on growth of individually reared *Daphnia magna* and further to consider the application of the equation

$$y = bx^k$$

to relative growth and variation in Cladocera.

Materials and Methods

Female *Daphnia magna* Straus. of several clones were employed. One clone was used for the major portion of the work. To determine whether or not the observed results were characteristic only of the one clone, some six others were tested. One of the latter was secured from Dr. A. M. Banta. All of the other clones, including the one first mentioned, were derived from ephippial eggs which may be traced to Banta's stocks.

Individual females were isolated within six hours of their release from the brood chambers of the mothers. These were measured and placed in separate vials containing thirty to thirty-five cubic centimeters of a culture medium. Banta's manure-soil medium (Banta, 1921) and oatmeal and wheat modifications were employed. More uniform results were obtained from the regular manure-soil medium than from modifications, as the results of one series of experiments indicate.

Where a modified culture medium was used, the animals were placed in old manure-soil medium and a drop of an oatmeal mixture or wheat infusion was added daily. Water was added to replace the fluid lost by evaporation. The oatmeal mixture was prepared by cooking rolled oats for a half hour in about twice the amount of water ordinarily used in making a porridge. The mixture was then strained through gauze and kept in a refrigerator until used. The wheat infusion was prepared by

Table I

Mean total lengths of female *Daphnia magna* of one clone during each of the pre-adult instars and the first adult for different classes of individuals. The classes are based on the number of pre-adult instars and the nature of the culture medium.

MEDIUM	MANURE-SOIL	OATMEAL MODIFICATION				
Number of Pre-adult Instars	5	5	6	7	8	
Number of Cases	19	8	29	39	5	
First Instar	0.85 ± 0.01	0.80 ± 0.01	0.84 ± 0.01	0.83 ± 0.01	0.77 ± 0.02	
Second Instar	1.09 ± 0.02	1.02 ± 0.01	1.00 ± 0.01	0.94 ± 0.01	0.86 ± 0.02	
Third Instar	1.39 ± 0.02	1.33 ± 0.03	1.17 ± 0.01	1.05 ± 0.01	0.99 ± 0.03	MEAN TOTAL LENGTH IN MM.
Fourth Instar	1.77 ± 0.02	1.70 ± 0.03	1.36 ± 0.02	1.19 ± 0.01	1.12 ± 0.04	
Fifth Instar	2.13 ± 0.02	2.06 ± 0.04	1.64 ± 0.02	1.38 ± 0.01	1.22 ± 0.05	
Sixth Instar	Adult 2.60 ± 0.02	Adult 2.56 ± 0.03	1.99 ± 0.02	1.69 ± 0.01	1.55 ± 0.10	
Seventh Instar			Adult 2.49 ± 0.02	2.08 ± 0.03	1.87 ± 0.09	
Eighth Instar				Adult 2.56 ± 0.03	2.20 ± 0.04	
Ninth Instar					Adult 2.52 ± 0.03	
Number of Young in First Brood	6.4 ± 0.3	6.4 ± 0.6	7.3 ± 0.2	8.6 ± 0.3	5.8 ± 0.8	
Number of Young in Second Brood	9.5 ± 0.5	9.4 ± 0.6	7.4 ± 0.3	7.1 ± 0.2	5.2 ± 1.0	

boiling wheat in water, decanting the fluid, and allowing this to stand open for several days before using. When the manure-soil medium was used exclusively, one-third of the fluid was removed semiweekly from each vial and replaced by fresh medium.

At the time of isolation of the individuals and after every moult each individual was placed in a watch glass together with a few drops of the culture medium. Just enough of a saturated solution of chloretone was added to bring about cessation of movement. The chloretone did not appear to have any detrimental effects. By means of an ocular micrometer the measurements as illustrated in Figure 2 were made. The three measurements consisted of total length exclusive of the spine, carapace length, and height. Camera lucida outline drawings were made during each instar for each of three animals. In addition to these measurements, note was taken as to the presence of eggs in the brood chamber. Within twenty-four hours after their release the young were removed from the vials and counted.

Size and shape change only at the time of moulting in this species. Repeated measurements of any dimension during a single instar always gave the same results. Agar (1930) pointed out this fact for *Daphnia carinata* and *Simocephalus gibbosus*. Such being the case, a single set of measurements suffice for each animal during any one instar.

All the experiments were carried out at room temperature (18°–23° C.).

Number of Pre-Adult Instars and Growth

The results of observations on the number of pre-adult instars, *i.e.*, the number of instars elapsing between the time of release of the individual female from the brood chamber of her mother and the appearance of eggs in its own brood chamber, and the mean total length of the animals during each are summarized in Table I. The data were segregated on the basis of the number of pre-adult instars and the culture medium used. The number of pre-adult instars varied for the animals reared in the oatmeal modification. For those reared on the standard manure-soil medium the number was constant. Twenty individuals only were used in the latter series, one of which died before reaching maturity.

The number of pre-adult instars above five may perhaps be explained on the basis of food deficiency. Great numbers of large ciliates were found in the modified medium. These probably reduced the number of smaller microörganisms that ordinarily would have been available as food to the *Daphnia*. The ciliates themselves were too large to be consumed. Conditions similar to this arose at a time when great numbers of the annelid *Aeolosoma* were found in the culture medium. At times

a culture medium seems to stimulate the adult females to produce great numbers of young, but this same lot of medium does not seem sufficient for the development of the young.

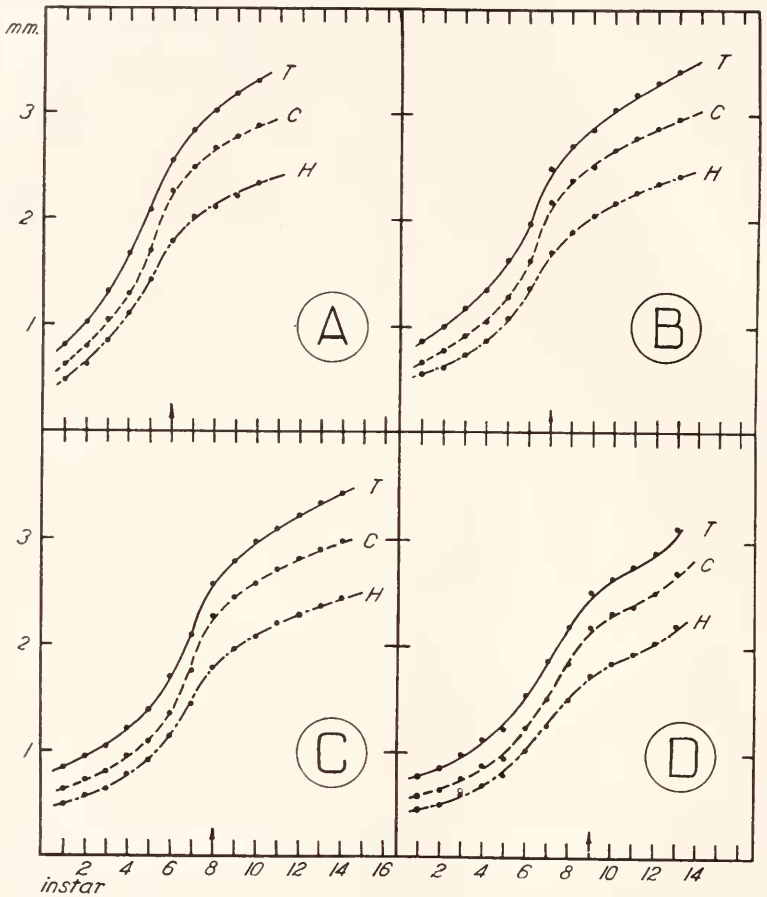

FIG. 3. Growth curves of different classes of individuals reared on the oatmeal modification; *A*—those animals with five pre-adult instars (7 individuals), *B*—six (18 individuals), *C*—seven (30 individuals), *D*—eight (5 individuals). *T*—total length; *C*—carapace length; *H*—height. The arrow indicates the first adult instar.

The animals used in the experiment with the modified medium were all released on the same day. The time taken to reach sexual maturity varied from six to ten days. The number of days corresponded approximately to the number of pre-adult instars in each case. The animals were all kept under identical conditions and the culture medium was from the same lot. The experiment using the standard manure-soil medium was begun several weeks later.

Table I brings out an interesting relation. The mean size for each group during the instar when eggs first appear in the brood chamber varies from 2.49 mm. to 2.60 millimeters. Apparently *Daphnia magna* must attain a certain size before becoming sexually mature. Singh-

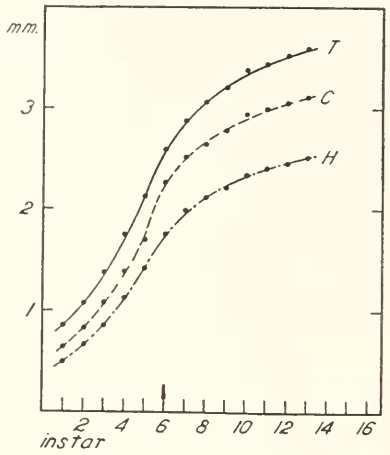

FIG. 4. Growth curves of a group of animals reared on unmodified manure-soil medium. These had five pre-adult instars (7 individuals). *T*—total length; *C*—carapace length; *H*—height. The arrow indicates the first adult instar.

Pruthi (1925, etc.) found that metamorphosis of mealworms took place only after the larvæ were full-grown.

Rammner (1930*b*) has found that eggs were produced after the fourth instar in *Daphnia magna*. After observation on well over a thousand individually reared females, the writer has never observed less than five. L. A. Brown has observed five pre-adult instars for this

TABLE II

Number of Individuals Primiparous During the Sixth to Ninth Instar

Clone	Sixth Instar	Seventh Instar	Eighth Instar	Ninth Instar	∞
B	4	10	4	2	0
C	8	3	1	0	1
D	7	4	0	0	0
E	9	1	1	0	0
F	6	11	2	0	0
G *	10	4	4	0	1

∞ Those living beyond the 10th instar without bearing eggs.
* Clone secured from Dr. A. M. Banta.

species (unpublished data). Rammner's smaller number may be due to some factor in the culture medium or perhaps to a genetic difference in his animals.

Figures 3 and 4 are growth curves constructed from data secured from animals included in Table I. The data used were taken only

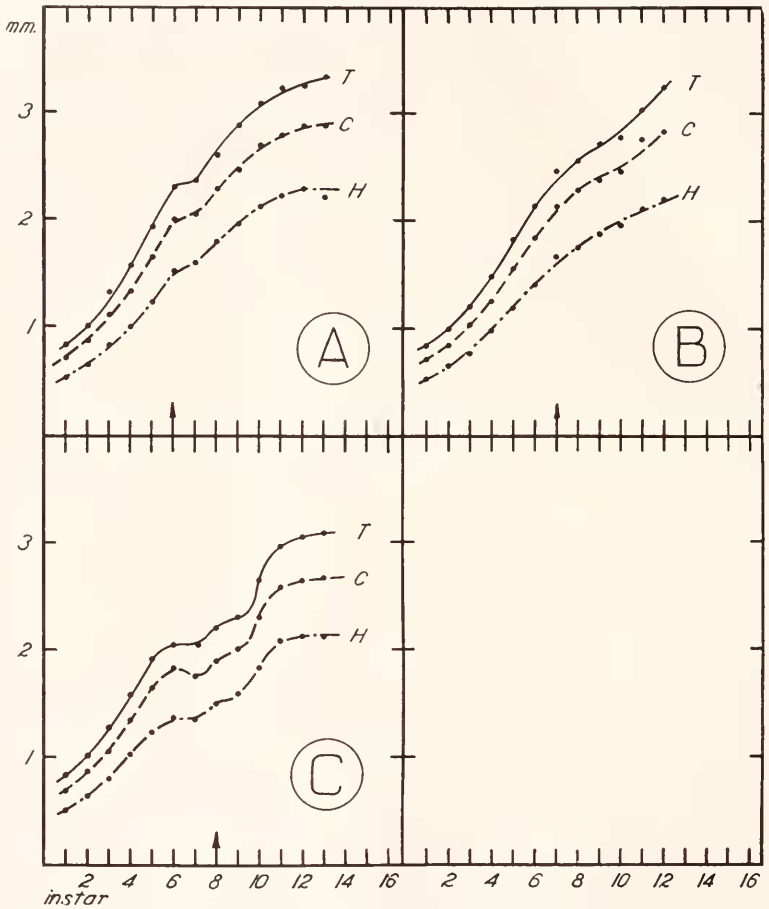

FIG. 5. Growth curves of three broodmates of clone *B*. Animal *A* had five pre-adult instars; *B*, six; and *C*, seven. *T*—total length; *C*—carapace length; *H*—height. Arrow indicates first adult instar.

from those animals which were still living during the last instar recorded on the graphs. All such are included. The inflection in the curves always occurs at a point which corresponds to the time of sexual maturity.

All the individuals used in the above experiments were of the same

clone. To determine whether or not the variation in the number of pre-adult instars was characteristic only of this clone, another series of experiments was performed using six other clones. Five of these were raised from ephippial eggs. A sixth clone was secured from Dr. A. M. Banta. Manure-soil medium and the wheat modification were employed in these tests. Table II gives the results. Examination of this

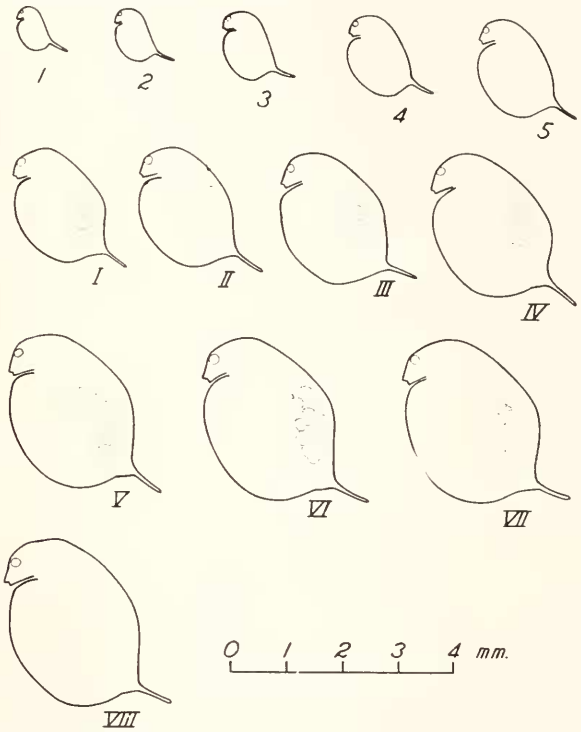

FIG. 6. Outline drawings of a single animal during each of the first thirteen instars. The animal is the one for which growth curves are shown in Figure 5*A*. The arabic numerals designate pre-adult instars; the Roman numerals—adult instars.

table shows that the variability in the number of pre-adult instars is characteristic of all clones used. Variation occurred to about the same extent in both media.

Two of the animals included in the above experiments lived for at least thirteen instars without bearing young. Ordinarily the ovary in the adult assumes a green color, especially toward the end of the instar. Microscopic examination did at no time reveal the development of the green color in the ovaries of either animal. In one of them growth did not seem retarded. Her total length during the thirteenth instar equaled

the average total length, during the same instar, of those primiparous in the sixth.

Individual growth curves for three brood mates of clone *B* are shown in Figure 5. Each of these as designated *A*, *B*, and *C*, bore its first clutch of eggs in the sixth, seventh, and eighth instars respectively. These were raised under the same conditions and at the same time, using the same lot of unmodified manure-soil medium. The measure-

TABLE III

Growth ratios for various classes of animals according to the nature of the culture medium, number of pre-adult instars, and clone

Instars	CLASS*							
	M6	M7	M8	M9	R6	B6	B7	B8
1– 2	1.27	1.16	1.13	1.11	1.26	1.24	1.19	1.25
2– 3	1.29	1.17	1.10	1.15	1.29	1.28	1.21	1.23
3– 4	1.27	1.14	1.17	1.14	1.27	1.19	1.23	1.24
4– 5	1.25	1.21	1.14	1.09	1.22	1.23	1.23	1.21
5– 6	1.24†	1.21	1.22	1.27	1.22†	1.19†	1.18	1.07
6– 7	1.10	1.26†	1.24	1.21	1.11	1.02	1.15†	1.00
7– 8	1.07	1.09	1.23†	1.18	1.07	1.10	1.04	1.08†
8– 9	1.05	1.06	1.08	1.15†	1.05	1.11	1.07	1.05
9–10	1.04	1.07	1.06	1.05	1.05	1.07	1.02	1.15
10–11		1.05	1.04	1.05	1.02	1.05	1.09	1.12
11–12		1.03	1.04	1.05	1.02	1.01	1.07	1.03
12–13		1.03	1.05	1.08	1.02	1.02		1.01
13–14			1.03					
Number of Animals	7	18	30	5	7	1	1	1

* Classes—M6, M7, M8, and M9 from clone *A* reared on modified medium and primiparous in the sixth, seventh, eighth, and ninth instars respectively. R6 from clone *A* and reared on the regular manure-soil medium, primiparous in the sixth instar. B6, B7, and B8 from clone *B*, primiparous in the sixth, seventh, and eighth instars respectively. This table is based on the same data as are Figs. 3, 4, and 5. The ratios are based on total length.

† Denotes instar during which animals were primiparous.

ments for these were made by means of camera-lucida drawings. Figure 6 is a reproduction of the series of camera-lucida drawings for animal *A*.

The irregularities in the number of pre-adult instars and in the growth of *Daphnia magna* as brought out above indicate that no law of growth such as "Brooks' Law" is valid under all circumstances. Table III brings the case out more clearly. This table gives the values of the ratio of the total length during each instar for each group to that

of the previous instar. These values correspond to the " Wachstumsquotienten " of Rammner (1930) and others. For those cases in which the individuals were primiparous in the sixth instar the value is fairly

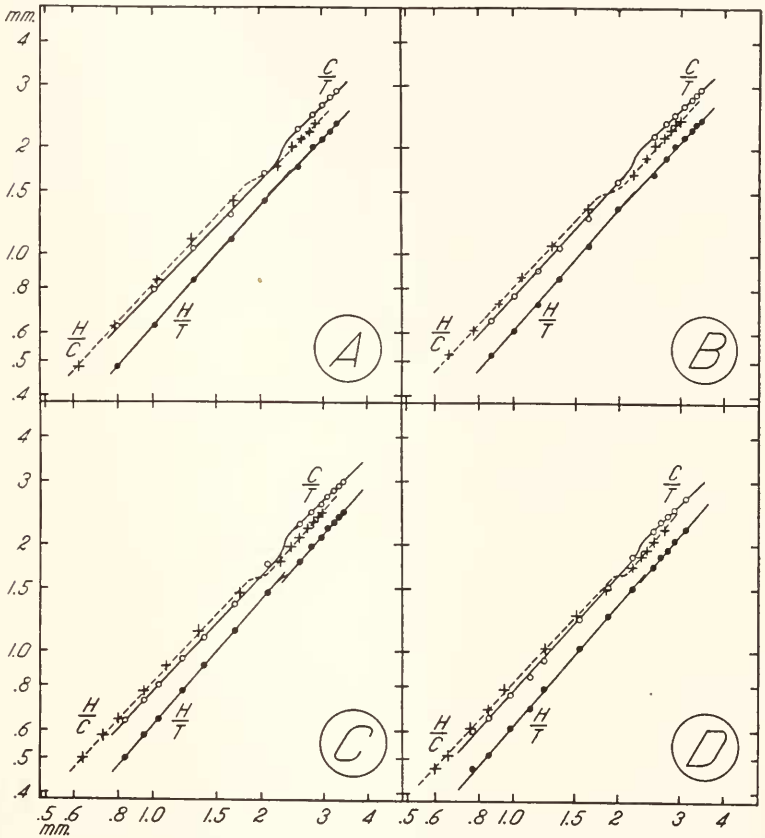

FIG. 7. *Log log* plots of the relations between carapace length and total length C/T, height and total length H/T, and height and carapace length H/C during each instar for different classes of animals reared on the oatmeal modification—the same for which growth curves are shown in Figure 3. The lines were drawn according to the calculated values of the constants given in Table IV. The breaks in the relations are coincident with sexual maturity. *A*—animals with five pre-adult instars (7 individuals), *B*—six (18 individuals), *C*—seven (30 individuals), and *D*—eight (5 individuals).

constant during the pre-adult stages. In all other instances the value is quite variable. After sexual maturity the value decreases considerably and approaches unity in old age. The validity of " Brooks' Law " with regard to *Daphnia magna* may therefore be considered to depend on the conditions of the individual and of the environment.

Relative Growth and Variation

The foregoing portion of this paper has brought out the wide irregularities in the general growth rate of individual *Daphnia magna*. In spite of these irregularities the relative growth of parts is quite constant. If the logarithm of the carapace length be plotted against the logarithm of the total length for each, two straight lines may be drawn—one through the points for the pre-adult instars and the other for the adult instars. The lines so drawn differ slightly in slope and in position (Figs. 7, 8, and 9). Such *log log* plots of height against total length

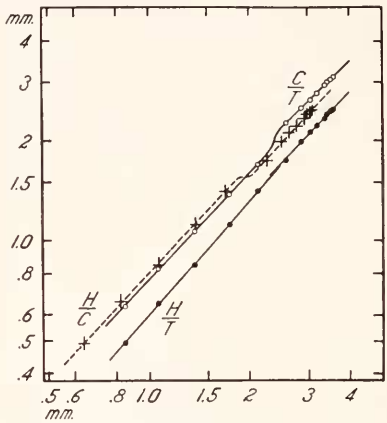

Fig. 8. *Log log* plots of the relations between carapace length and total length C/T, height and total length H/T, and height and carapace length H/C during each instar for a group of animals reared on unmodified manure-soil medium—the same for which growth curves are shown in Figure 4. The lines were drawn according to the calculated values of the constants given in Table IV. The breaks in the relations are coincident with sexual maturity.

and against carapace length show similar characteristics. These linear relations can be expressed as

$$y = bx^k,$$

where b is a constant and k is the "differential growth ratio" of y compared with x. Huxley (1924, etc.) [2] has found that a large number of organs obey this law. Hersh (1928, 1931) has shown that the facet numbers in the dorsal and ventral lobes of bar-eyed *Drosophila* conform to this equation. Robb (1929) has applied this relation to relative growth of organs in mammals and found it satisfactory.

[2] For an elucidating treatise on relative growth see Huxley "Problems of Relative Growth" (Methuen Co., London, 1932). This work became available to the author after having submitted the present paper to the editors.

TABLE IV

Values of the constants b and k during pre-adult and adult instars for various classes of *Daphnia magna* based on the nature of the culture medium, number of pre-adult instars, and clone. These relations are shown graphically in Figs. 7, 8, and 9.

TOTAL LENGTH (x) CARAPACE LENGTH (y)					TOTAL LENGTH (x) HEIGHT (y)				CARAPACE LENGTH (x) HEIGHT (y)				NUMBER OF ANIMALS
Pre-adult			Adult		Pre-adult		Adult		Pre-adult		Adult		
Class*	k	b	k	b	k	b	k	b	k	b	k	b	
M6	1.03	0.78	0.99	0.88	1.12	0.62	1.03	0.67	1.09	0.81	1.04	0.77	7
M7	1.07	0.77	0.96	0.91	1.15	0.62	1.07	0.65	1.08	0.82	1.12	0.72	18
M8	1.08	0.77	1.02	0.86	1.16	0.62	1.15	0.60	1.08	0.82	1.13	0.71	30
M9	1.08	0.77	0.95	0.92	1.14	0.62	1.14	0.61	1.06	0.81	1.20	0.68	5
R6	1.06	0.76	0.97	0.90	1.13	0.60	1.05	0.65	1.07	0.80	1.08	0.73	7
B6	1.01	0.84	1.02	0.85	1.01	0.63	1.06	0.64	1.00	0.75	1.04	0.76	1
B7	1.02	0.85	1.07	0.82	1.05	0.64	1.10	0.62	1.03	0.76	1.03	0.76	1
B8	1.07	0.83	1.01	0.86	1.10	0.61	1.05	0.66	1.03	0.75	1.05	0.77	1

* Classes—M6, animals of clone *A* raised on modified medium and primiparous during the sixth instar; M7, M8, M9, as M6 but primiparous during the seventh, eighth, and ninth instars respectively. R6, animals reared on the regular manure-soil medium and primiparous during the sixth instar. B6, B7, B8, individuals of clone *B* primiparous during the sixth, seventh, and eighth instars respectively. The classes are the same as those in Table III and in Figs. 3, 4, 5, 7, 8, and 9 and the values of the constants are based on the same data.

An interesting feature coming out of this study is that relative growth changes at sexual maturity. This may be seen on examination of any one of the *log log* graphs. The change is much more distinct in clone *A* (Figs. 7 and 8). The change in clone *B* is less discernible

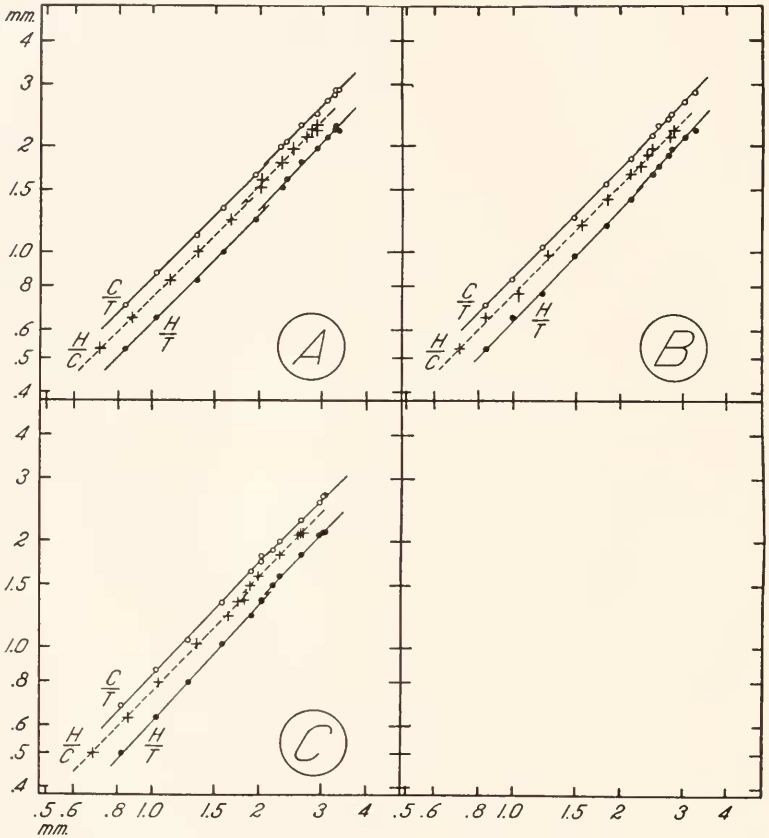

FIG. 9. *Log log* plots of the relations between carapace length and total length C/T, height and total length H/T, and height and carapace length H/C during each instar for three individual broodmates of clone *B*—the same for which growth curves are shown in Figure 5. The lines were drawn according to the calculated values of the constants given in Table IV. The breaks in the relations are coincident with sexual maturity. Animal *A* had five pre-adult instars, *B* six, and *C* seven.

(Fig. 9). Table IV gives the values of the constants b and k for both clones. These were computed by the method of averages. Since all points on any one graph represent the same number of cases, the cal-

culated values of the constants are practically as accurate as those secured by a more elaborate method.

Huxley (1927) has suggested that heterogony in *Maia* begins at sexual maturity. He also noted that this is probably true for male *Gammarus*. Examination of Figure 1 in the same report shows a change in relative growth of the large chela as against the rest of the body in *Uca pugnax*. Huxley makes no mention as to its significance. Robb (1929) has pointed out that a change takes place in the relative growth of various organs and suggests that another factor becomes involved. These changes are apparently coincident with sexual maturity.

Since the value of k approximates unity for all above relations, both for pre-adult and adult instars of *Daphnia magna,* and the value of b for each relation varies only over a small range, the animal does not change in proportions, to any great extent, during growth. Wesenberg-Lund (1926) writes that variations in *D. magna* of Denmark are insignificant. This condition is therefore as expected.

In a great many Cladocera pronounced variations occur. Rammner (1927) has discussed several methods for their study. As far as the writer is aware, no one has considered applying the equation

$$y = bx^k$$

in such studies.

Masses of data on variation have been collected by various workers on several species (Werner, 1924; Rammner, 1926; Heberer, 1928). The data as presented by these workers do not allow of the proper manipulation for testing the validity of the equation for the purpose. Were the original data available, a satisfactory test might be made. Rammner's (1928) data on individually reared *Chydorus sphæricus* and *Pleuroxus trigonellus* seem quite irregular. Woltereck's (1925) data on individually reared *Daphnia cucullata* seem satisfactory for the pre-adult instars. In *log log* plots of the head length against the body length a break in the relations appears in about the middle of the pre-adult instar range and another at sexual maturity. The first change seems likely to affect only the value of the constant b in the equation while k remains approximately the same. The second change would probably affect the values of both constants. The values of the constants for the adult instars cannot be determined, since the data includes measurements for only one and sometimes two adult instars. Different varieties give different values for the constants. The general trend of the relations is the same.

The advantage of applying the equation

$$y = bx^k$$

to data on variation in Cladocera is that the direction of variation may be expressed numerically in the constants b and k. The data employed could be taken from preserved material such as that used by Werner and others. Huxley and his coworkers have used this method in the study of heterogeny in Crustacea with apparent success. Collections from several localities, as well as those made in the same locality at different seasons, might thus be readily analysed and compared.

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Summary

Observations as to the number of pre-adult instars have been made on over 200 individually reared female *Daphnia magna* of seven clones. In all cases measurements of the total length during each instar were taken. For well over a hundred individuals measurements of carapace length and height were taken in addition to those of total length.

The number of pre-adult instars varied upward from five. This variation was found in all clones tested.

Growth curves have been constructed for various groups based on the number of pre-adult instars. The inflection in the growth curve of any dimension in any group coincides with the time of sexual maturity.

" Brooks' Law " holds only for those groups which were primiparous during the sixth instar and then only approximately.

Relative growth in the dimensions studied, x and y, may be expressed by the equation

$$y = bx^k.$$

Relative growth changes at sexual maturity, *i.e.*, a change occurs in the values of the constants b and k.

The above equation may perhaps be used to advantage in the study of variation in other Cladocera. By the use of this equation the direction of variation can be given numerical values. Comparisons of differ-

ent races and varieties, both seasonal and geographic, may be readily made on this basis.

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